Vegetative Anatomy of *Carpodetus serratus* Forst.

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Carpodetus serratus is a small tree common throughout the New Zealand lowlands. It was first described in *Characteres Genera Plantarum*, by J. R and G. Forster, in 1776. The genus has been assigned to the Saxifragaceae (e.g., 31) but it is one of those transferred by Hutchinson (19) to his new family Escalloniaceae in the order Cunoniales, since he considers that woody genera should be separated from herbaceous Saxifragaceae. In the present flora (7) *Carpodetus* is said to be monotypic and endemic in New Zealand, but both Schlechter and Reeder (25) have referred species from New Guinea and adjacent areas to it, Reeder describing or mentioning as many as nine.

Apart from brief reference by Solereder (31) nothing appears to have been published respecting the anatomy of any of these species. This paper records salient features of the vegetative parts of *C. serratus* and pays special attention to those considered to be significant in phylogenetic classification

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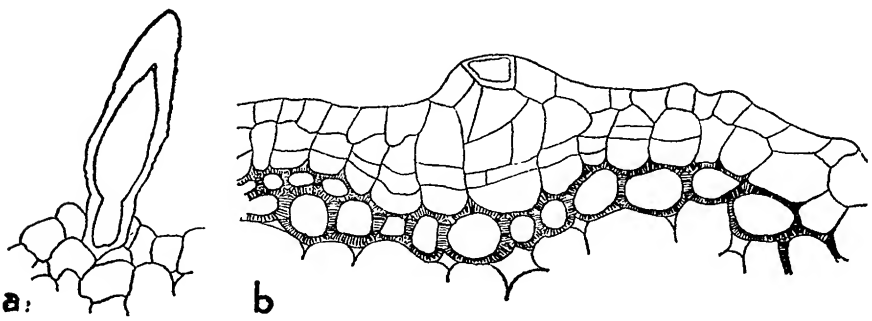
Stem Anatomy

Primary Structure

The primary stem structure (Pl. 38, A) has few noteworthy features. The epidermis bears frequent unicellular cutinised hairs (Fig. 1a)



Text Fig. 1—(a) L.S. hair on young stem. (× 235.) (b) T.S. portion of outer part of young stem showing origin of phellogen beneath a hair base (× 240)

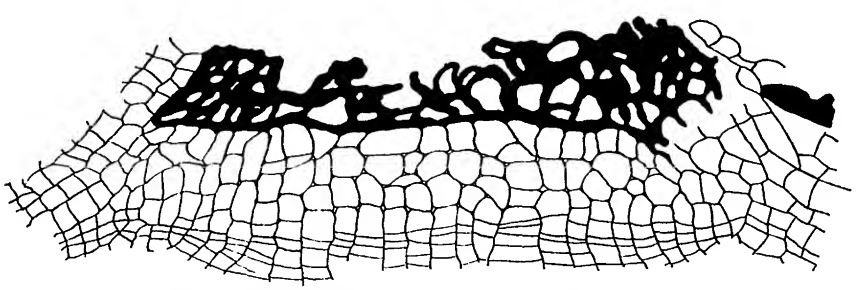
and at wide intervals stomata of the normal type described by Haberlandt (18) for *Narcissus biflorus* and *Helleborus* As in woody Angiosperms generally (11), there is not a typical endodermis, but a more or less definite ring of cells about the stele is regarded as such, since

in very young seedlings Caspary's bands were seen in this layer. The bundles of primary vascular tissue vary in size, the median leaf trace bundles being the largest, and showing marked radial arrangement of the primary xylem—a condition attributed by Esau (13) to repeated periclinal division of the procambial cells. Wood elements comprise annular, spiral, scalariform and dotted types. The spiral, annular and some of the scalariform and dotted cells are tracheids, but others of the last two types have end walls and are thought to be vessel segments. This possession of tracheids in primary, but not in secondary wood, is not abnormal (14). The primary phloem, in addition to sieve tubes, companion cells and parenchyma, contains peripherally groups of 2–10 small angular cells comparable with those described by Artschwager (1) from the potato, though in the present case consisting only of what he terms "conducting parenchyma." These conducting parenchyma groups also occur in the stele between the collateral primary bundles. When traced longitudinally they were found to branch and anastomose and ultimately to fuse with the collateral bundles. The pith is solid and lignifies early.

The leaves are alternate with one-half phyllotaxis. The node Pl. 38, A) is trilacunar with the lateral traces each about a quarter of the circumference of the stem away from the larger median trace. These features of leaf arrangement and vascular supply are regarded as primitive (10, 29, 30), but the leaf itself, since it is not compound and lacks stipules, is not of the most primitive form in Angiosperms (10, 19).

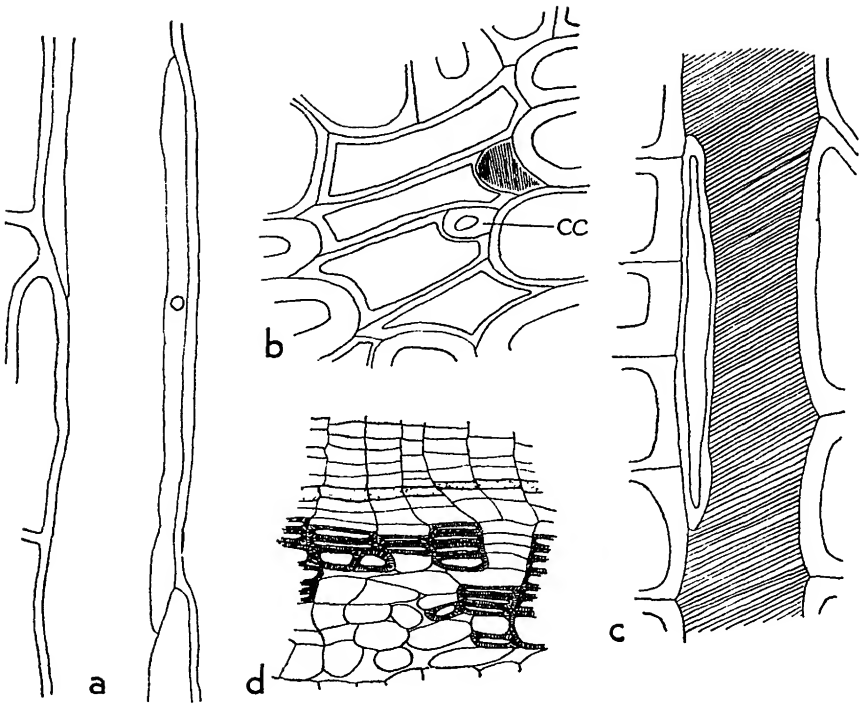
Secondary Structure

The phellogen arises in the cortical layer immediately beneath the epidermis; appearing first, as is usual (11), at points where lenticels will develop. These are initiated mainly under hairs (Fig. 1b), stomata having little guiding and no limiting influence on their formation. The lenticels (Fig. 2) are small and rather greater in



TEXT FIG. 2—T.S. lenticel in mature stem. (× 110)

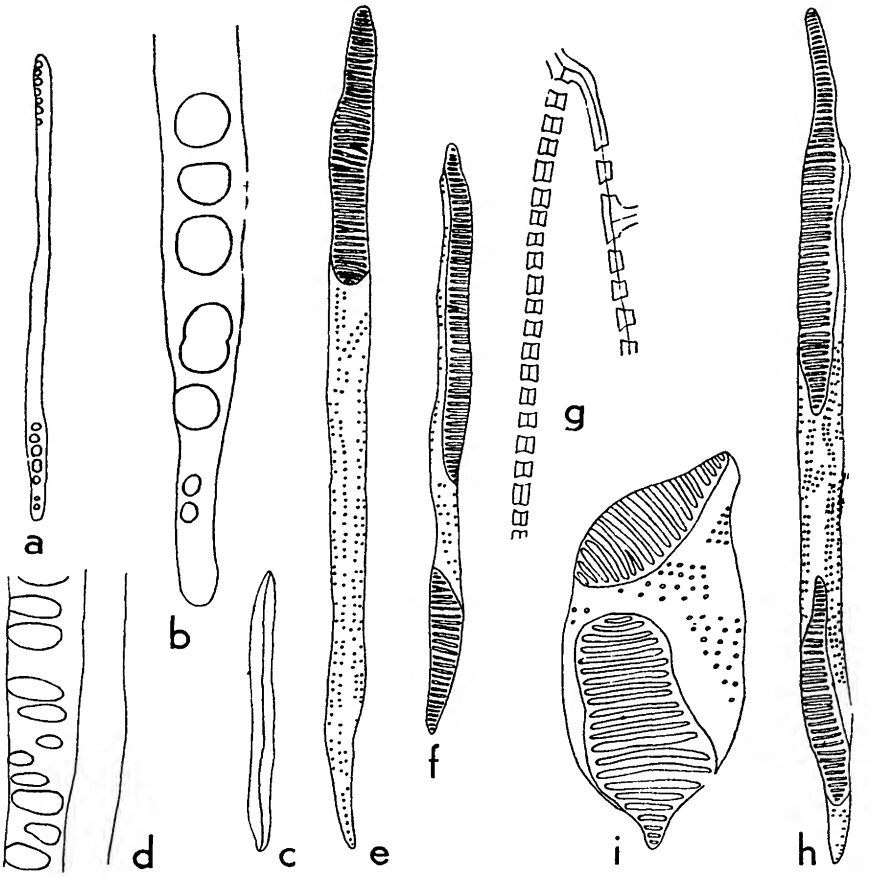
transverse than in longitudinal extent. This is considered to be a primitive orientation (32). The complementary tissue is compact, the structure corresponding with Devaux's second type (9). The original phellogen persists throughout life of the tree, dividing slowly and maintaining only a thin cork layer seldom more than ten cells thick (Pl. 38, B). However, a wide zone of phelloderm is formed which matures into irregular masses of radially arranged stone cells (Fig.



TEXT FIG. 3—(a) L.S. secondary phloem showing companion cells and a sieve tube. (× 440.) (b) T.S. small region of lignified phloem showing a lignified companion cell *c.c.* (× 665.) (c) L.S. lignified phloem to show lignified companion cell and a dead sieve tube. (× 425.) (d) T.S. portion of periderm in mature stem showing phellogen (stippled) and phelloderm stone cells. (× 140.)

3d) separated by loosely packed parenchyma cells which increase by radial divisions to accommodate the tangential stresses set up by the expanding stele. Cells of the persisting primary cortex show still more active radial division. Like the phelloderm this tissue becomes partially converted to stone cells. Lignified primary cortical cells can be distinguished from the phelloderm stone cells since in the former lignification occurs only after radial divisions have given these cells a marked tangential seriation.

In cross section the secondary phloem recalls the well-known arrangement of *Tilia* Expanding multiseriate rays separate tapering masses of sieve-tubes, companion cells, phloem parenchyma and uniseriate rays, but there is no fibre in the active phloem. The older phloem, however, is converted into tapering tongues of sclerenchyma, and small patches of lignified cells also appear in the intervening ray tissue. Sieve-tube elements are narrow and tapered without definite end walls (Fig. 4a). The overlapping ends of successive elements are interconnected by several sieve plates, and smaller sieve plates occur elsewhere along the cell where it comes laterally in contact with another sieve-tube (Fig. 4d). They conform with Hemenway's first type (12) which is considered a primitive one (20). Callus



TEXT FIG. 4—(a, c) Complete sieve tubes. (× 80.) (b) Lower end of (a) showing sieve plates. (× 400.) (d) Portion (indicated) of (c) showing sieve plates on lateral wall. (× 400.) (e, f) Vessel segments from stem wood. (× 85.) (g) L.S. vessel segment tip to show bordered perforations (left), and nature of pitting between vessels and wood parenchyma (right). (× 680.) (h) Vessel segment from wood of exposed root. (× 90.) (i) Vessel segment from wood of buried root. (× 135.)

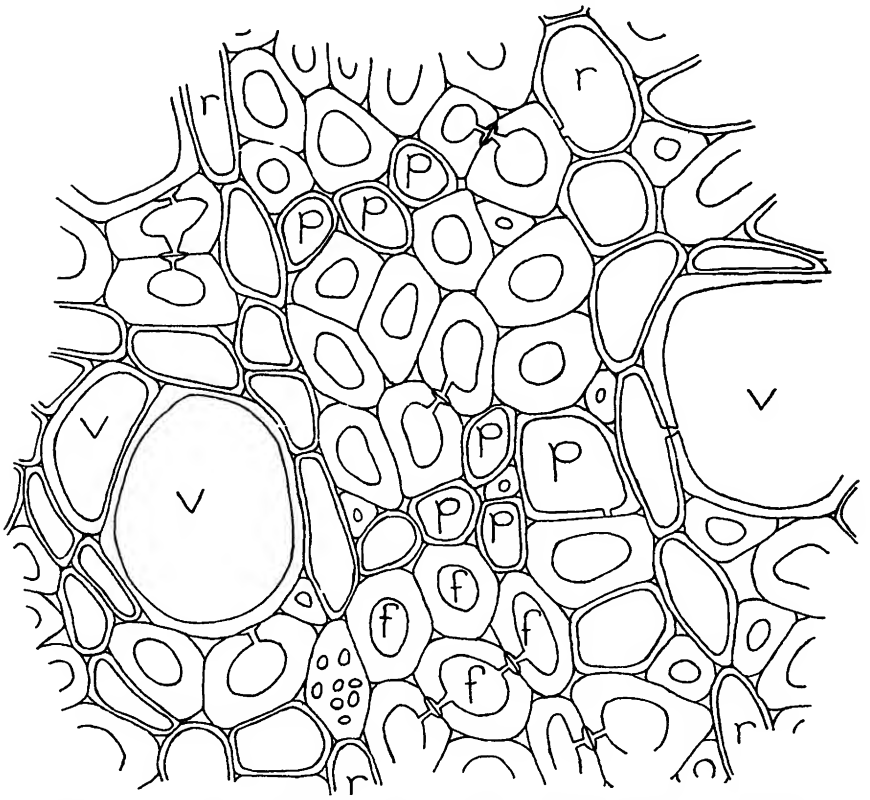
was not observed, but the material was all collected in winter, and it is possible that it might be present at other times of the year since it does not necessarily persist after death of the cell (12). Each sieve-tube element usually has several companion cells which are remote from one another (Fig 3a). Phloem parenchyma is abundant. Between sieve-tubes and parenchyma cells are numerous pits that are often large. Uniseriate rays extend from the wood without change of cell structure except that the walls are not lignified in the phloem. The multiseriate rays are derived from compactly arranged rectangular initials. The ray cells soon round off, then broaden tangentially, and finally divide into tangential rows of cells in the same manner as cortical parenchyma. In these rays only scattered cell

groups become lignified, whereas nearly all parenchyma accompanying the vertical phloem elements is ultimately converted to stone cells. Sieve-tubes do not lignify, but neither they nor any unlignified parenchyma are greatly crushed. Apparently the thin cork and the capacity of cortex and periderm cells for radial division prevent the usual pressure developing between secondary wood and bark. It is noteworthy that a good many of the old companion cells do lignify (Figs. 3b, 3c), a phenomenon that does not appear to have been observed previously, it being usual for these cells to die and collapse along with their sister sieve-tube element (12).

The secondary wood is almost white in colour, with obscure growth rings, but prominent rays along which it invariably splits as it dries. The wood is diffuse-porous (Pl. 39, A), annual ring boundaries being defined by the contrast between summer and spring wood vessel diameters. Ray cells broaden tangentially in the summer wood. No tracheids are present, the vertical conducting cells all being vessels (Figs. 4e, 4f). By Chattaway's (6) standards these vessels are very numerous, and their thin-walled, angular segments have a " small " tangential diameter and are " extremely long." (For actual measurements see Table of Descriptions.) Segment end walls are very oblique, often with tails, and with numerous narrow, fully-bordered perforations (Fig. 4g) which are always scalariform. The vessel pitting is opposite. Except for this last feature, which is considered slightly more advanced than sclariform pitting, the vessel segment is primitive in every respect (14, 15, 16). Very oblique end walls are the rule in woods such as *Carpodetus* which are not storied (5). The bulk of the tissue between the vessels is comprised of fibres (Fig. 5), which by Chattaway's standards are " very long " and " thin " walled. Pitting is fairly evenly distributed, on all walls, the pit chambers easily visible, borders strongly developed, and the inner apertures narrow and included. Such fibres are classed as fibre-tracheids (26) and considered to be a somewhat primitive type (2). As Priestley (23) has established as generally true, pits are not formed between fibres and other elements (Fig. 5). Vertical parenchyma are diffuse (Fig. 5), the cells in similar vertical series to the phloem parenchyma. Ray structure conforms with Krib's (22) heterogeneous type I. which both he and Barghoorn (3, 4) consider the most primitive in Angiosperms. In this type the uniseriate rays are high and composed of vertically elongated cells. The multiseriate rays possess high uniseriate tips identical with the uniseriate rays, and are in their multiseriate parts parallel-sided with elongated lateral cells (Pl. 39, B). Primary multiseriate rays are, of course, of interfascicular origin. Secondary ones were observed to arise by two of the methods described by Barghoorn (3, 4)—i.e., by widening of a uniseriate ray or by coalescence of several such rays, and they are occasionally split apparently by changeover from ray to fusiform initials in the cambium. On Chattaway's standards these rays are "very broad" and "extremely high."

Table of Description of Secondary Wood

A description of wood in *C. serratus* has been prepared following the plan suggested by Rendle and Clarke (27, 28). It is based on four trees between 30 and 50 years old growing in a variety of situa-



TEXT FIG. 5—T.S secondary wood of stem. Typical cells are lettered: vessels (v), vertical parenchyma (p), fibres (f), uniseriate rays (r). (× 700.)

tions in Otago and Southland. From each tree five samples were selected at equal intervals from the base of the trunk up to branches about five years old, care being taken to keep sufficiently far from the pith to avoid variability described by Desch (8). It should be noted that Barghoorn (4) states that ray heights and widths should be used with great care, if at all, in wood identification.

STEM WOOD OF *Carpodetus serratus* FORST.

Vessels:			
(a) Measurements:	Mean	Standard Deviation	S.D. of Means
Total Segment Length	1041.0μ	220.21μ	88.991μ
Radial Diameter	47.9μ	12.677μ	5.6909μ
Tangential Diameter	35.1μ	10.809μ	3.9089μ

(25 measurements of each from each sample—total: 500 of each)

(b) Number. Vessels more or less evenly distributed. Range from 40–110, but mostly 50–80 pores or groups per square millimetre. (2 counts from each sample—total: 40)

(c) Grouping: Vessels solitary or in groups of 2–4, about 60% solitary and about 35% in pairs. (60 counts from each sample—total: 1200)

Fibres:

Mean Fibre Length = 1653.0μ
Standard Deviation = 301.1μ
Standard Deviation of Means = 166.2μ
(25 measurements per sample—total: 500)

Rays.

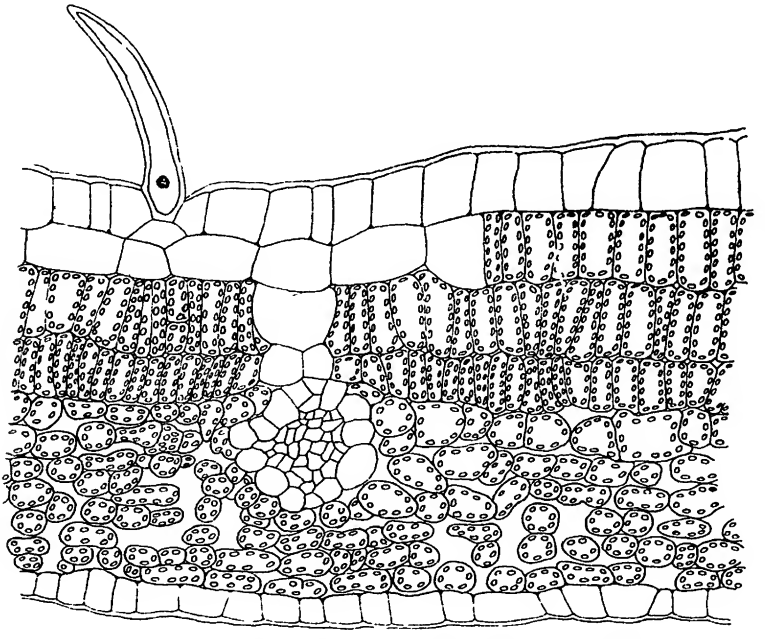
(a) Height: Multiseriate rays vary from 450μ–13200μ with about 60% from 1400μ–3000μ. Uniseriate rays vary evenly from 150μ–4150μ. (25 measurements per sample—total: 500)

(b) Width: About 75% are uniseriate. The multiseriate rays vary from 2–16 cells in width, with about 55% from 5–8 cells, and about 15% 2 cells wide. (50 measurements per sample—total: 1000)

Root Anatomy

The root system is composed of laterals, there being no persistent tap-root. These roots vary from 4-arch to polyarch, and always contain some pith which eventually lignifies. The initial phellogen forms well out in the cortex, and as in the stem is persistent and forms much phelloderm. There is little lignification of the phelloderm, but an almost complete sclerenchyma ring is formed further in by lignification of the old phloem parenchyma, outer parts of many phloem rays and the inner layers of the cortex. (Pl. 38, C.)

Secondary wood in roots that are exposed above the ground appears to differ from stem wood only in having broader rays (Pl. 39, C) (Fig. 4h), but subterranean roots have much larger vessels and correspondingly narrower multiseriate rays, fewer and thinner-walled fibres and more abundant vertical wood parenchyma (Pl. 39, D). Vessel segments in buried roots are shorter, including some very short vessels (Fig. 4i), a form never found in stems, and growth rings are more obscure The precise extent of histological differences between stem and root wood, and between exposed and buried root wood is the subject of a separate investigation, and no statistical data will be presented here



Text Fig. 6—T.S. part of an adult leaf. (× 250.)

LEAF ANATOMY

The three leaf traces unite in the petiole to form the usual arc of vascular tissue. This has no sclerenchyma associated with it, but the midrib and main veins possess a sclerenchyma sheath. The principal features of the lamina are shown in Fig. 6. The uppermost layer of palisade mesophyll, which amounts in all to from 2–4 layers, is intermittently replaced by clear hypodermal cells, as has been noted by Solereder (31). This hypodermis is not responsible for the mottled appearance of the foliage. This is due to a higher chlorophyll content of the mesophyll adjacent to large veins. Hairs and stomata are of the type already described from the stem, the latter being without subsidiary cells and confined to the lower epidermis. *C. serratus* is one of the New Zealand trees which possesses smaller leaves in juvenile than in adult trees. Juvenile leaves do not possess hypodermis and have no more than two palisade layers. Unpublished work by Johnston (21) has established that they have a closer vein network and more stomata per unit area than adult leaves.

DISCUSSION AND SUMMARY

The fullest account of wood structure in the Cunoniales is by Record (24), who states that the Escalloniaceae are the only family in the order which combine conspicuously large rays with scalariform vessel perforations and strongly bordered pits in the wood fibres. The existence of all these features in *C. serratus* confirms the classification of the genus in that family. The Cunoniales occupies an early place in Hutchinson's evolutionary tree for woody Dicotyledons. The vegetative anatomy of *C. serratus* confirms that position, since this species exhibits a primitive condition in almost every feature to which phylogenetic significance has been attached—viz.:

(a) Unstoried wood.

(b) Vessel segments thin walled, angular, long and narrow with very oblique end walls often tailed, and numerous narrow, fully-bordered perforations which are exclusively scalariform.

(c) Fibres of the fibre-tracheid type.

(d) A ray system conforming to Krib's heterogeneous type I.

(e) Apotracheal wood parenchyma.

(f) Long, tapered sieve tubes interconnected by several sieve plates.

(g) A trilacunar node.

(h) Leaf trace insertions in contact.

(i) Open bundle system.

Features which show a slight evolutionary advance are absence of tracheids in secondary wood, and opposite pitting of vessels. It has been contended that diffuse-porous woods are primitive, but Gilbert (17) points out that it can hardly be claimed that there is a general advance towards ring-porosity since this feature is confined to trees of the N. Temperate zone

The cortical system in both stem and root is characterised by a phellogen arising near the exterior and producing little cork but

much phelloderm. The phelloderm, though partially converted to stone cells in the stem, retains great tangential elasticity through radial division of its parenchyma. Old secondary phloem thus persists uncrushed, and certain companion cells therein undergo lignification along with the phloem parenchyma—a most unusual occurrence.

The leaf is of a normal mesophytic type. Adult leaves possess an intermittent colourless hypodermal layer. Attention is drawn to the fact that though there are substantial differences, mainly in size and frequency of component elements, between stem and buried root wood, these differences largely disappear if the root is uncovered.

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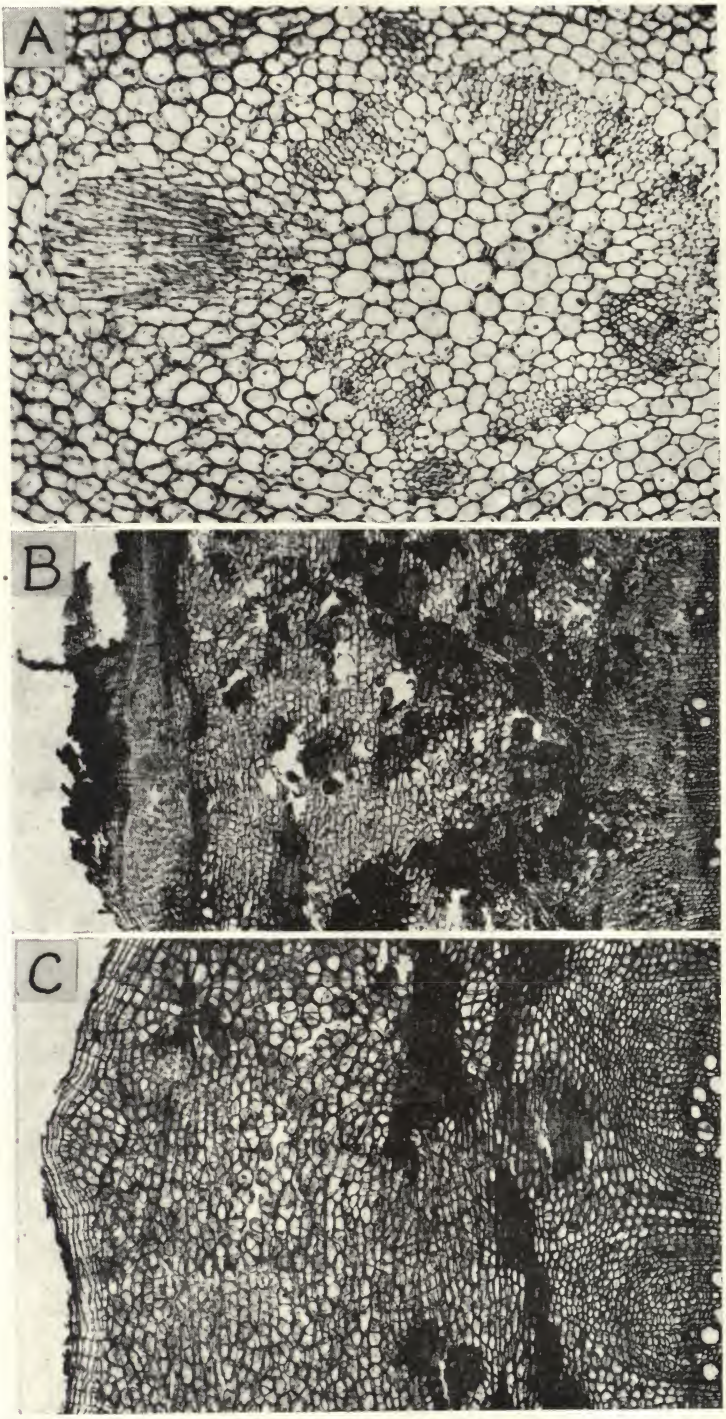

A. T.S. stem of seedling showing leaf traces. (× 100.)
B. T.S. bark of mature plant showing living and lignified phloem, lignified and non-lignified cortical cells, phelloderm and lenticel. (× 35.)
C. T.S. bark from subterranean root. Shows cork, phelloderm, lignified zone, and living phloem. (× 48.)

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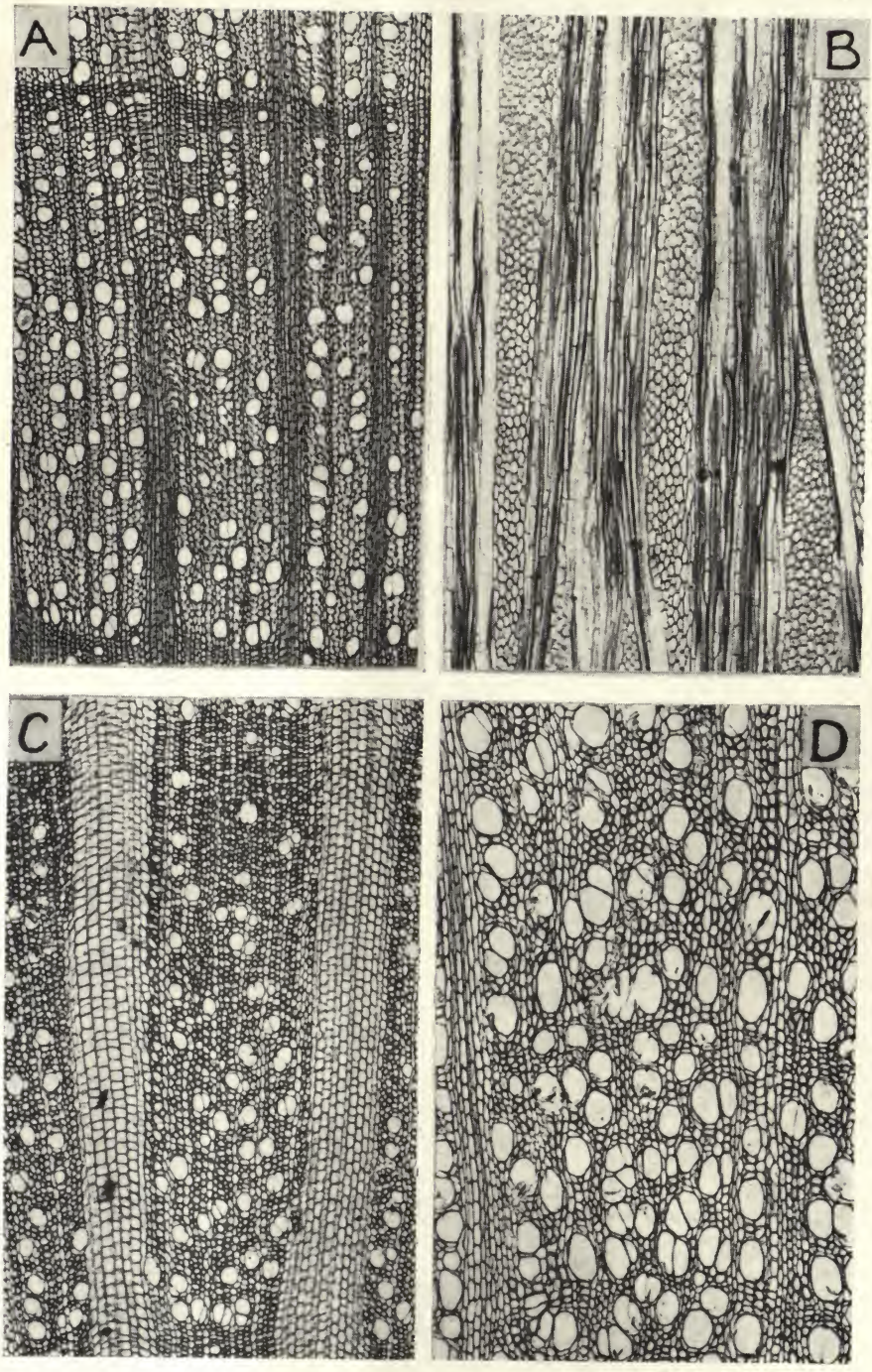

A. T.S. secondary xylem of stem, showing one annual ring. (× 43.)
B. L.S. secondary xylem of stem showing multiseriate and uniseriate rays. (× 43.)
C. T.S. secondary xylem of exposed root showing one annual ring. (× 43.)
D. T,S. secondary xylem of buried root. (× 43.)

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